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REGENERATIONAL LEG ASYMMETRY IN DAMAGED *TROGULUS NEPAEFORMIS* (SCOPOLI 1763) (OPILIONES, TROGULIDAE)

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ABSTRACT. Among the trogulid harvestman *Trogulus nepaeformis* (Scopoli 1763) collected from sixty localities in Slovenia and northeastern Italy we found many individuals with evidence of old leg injuries. In a few localities, injured individuals accounted for 30% of the total. In non-autotomizing trogulids, in vivo damage to leg articles is characterized by rounded regeneration of the stumps with pseudonormal terminal chaetotaxy, in some cases including a secondary claw. This damage, probably caused by shrews, was considered appropriate for analysis of the regenerational asymmetry, or RA, of legs. In 169 available regenerated specimens, the lengths of preserved articles on the damaged legs were compared to those on the undamaged ones. In the damaged specimens, the range of leg article RA was significantly larger in comparison to undamaged specimens. This is considered to be a direct consequence of the regenerative processes in the leg stumps. The damage was most frequent in 2nd leg, followed by 1st, 3rd and 4th, indicating that such wounds were not stochastic, and probably appeared during the forward motion of the troguli. The stomach contents of 204 shrews were examined and the remains of *T. nepaeformis* were found in two individuals demonstrating for the first time that shrews do feed on this species.

Keywords: Leg damage, regeneration, regenerational asymmetry, predation, shrews

The genus *Trogulus* is known as taxonomically the most difficult of the European harvestmen (Martens 1988), but is of particular interest because trogulids do not autotomize legs and individuals with damaged and healed legs can be found. Shrews and hedgehogs have been reported to prey on harvestmen although the harvestmen species have rarely been mentioned (Yalden 1976; Churchfield et al. 1991; Mitov 1995a; Haberl 2002). Prior to this study, troguli have not been explicitly reported to have leg stumps nor to be preyed upon by insectivores.

Matching asymmetry is defined as the asymmetry of two separate structures, one on each side of the body, existing as mirror images of each other (Mardia et al. 2000; Klingenberg et al. 2002). Fluctuating asymmetry (FA) relies on small differences between corresponding left and right body parts, R-L. The R-L items are normally distributed about the mean, which is not significantly different from the zero value. FA has often been used in detecting stresses and indicating the individual condition of organisms (Palmer & Strobeck 1986; Klingenberg et al. 2002). In cases of directional asymmetry (DA), the R-L is normally distributed about the mean, but the mean departs significantly from zero, while in antisymmetry, AS, the R-L is more or less bimodally distributed (Palmer & Strobeck 1992). Regenerational asymmetry (RA) arises most likely from a single event during ontogeny (Uetz et al. 1996), and in stochastical injuries, the R-L are expected to be distributed in the same way as FA.

The absence of leg autotomy in troguli presented the opportunity to study the impact of damage on the leg asymmetry within the opilionid *T. nepaeformis*. Most of the in vivo injuries in *T. nepaeformis* appeared to be caused by insectivores and were most frequent in the most exposed second legs. Our goals were to analyze the impact of in vivo leg damage on the RA of their limbs, and to check whether shrews are causing this damage in troguli.

METHODS

The RA analysis dealt with 169 damaged *T. nepaeformis* (71 males, 98 females) from 29 localities in western Slovenia and north-eastern Italy (range 13°10′–14°50′E, 45°30′–46°50′N). Most of the damaged specimens were collected in Korte (13°39′38″E, 45°29′20″N), Idrija (14°1′59″E, 46°0′13″N) and Tarcento (13°16′01″E, 46°11′54″N). From these localities we also collected undamaged specimens (39 males, 57 females). We analyzed only those damaged individuals that had a single regenerated leg with the opposite leg undamaged. Freshly injured individuals, those missing entire articles, and four with abnormally elongated secondary end-articles were not included.

We measured legs by laying them out on a slide in a lateral position and covering them with a second slide. If necessary, the upper slide was additionally loaded to press the leg in this position. Leg scanning was done under a Nikon SMZ-2T binocular microscope using a Eurocam (Euromex, Netherlands) digital camera connected to a personal computer. The lengths of the articles (Fig. 1) were measured using the TPS Dig program (Rohlf 2001). In testing RA, 19 of 30 leg articles with at least three items each were analyzed.

Two hundred and four soricids from six localities in the same area in Slovenia were investigated for their stomach contents by heating the stomach contents in 10% KOH and examining chitinous remains under a microscope.

Statistical analyses were carried out separately in the damaged and undamaged adult individuals, and in both sexes. Repeatability measurements were carried out on 14 characters of 67 randomly chosen damaged individuals. A mixed-model ANOVA was used for estimating asymmetry relative to measurement error (individual interaction X side), using Palmer's (1994) approach. The directional asymmetry (DA) was tested with a one-sample t-test, antisymmetry (AS) by using measures of platykurtism, and departures from normality with a one-sample Kolmogorov-Smirnov test. One outlier, exhibiting extreme

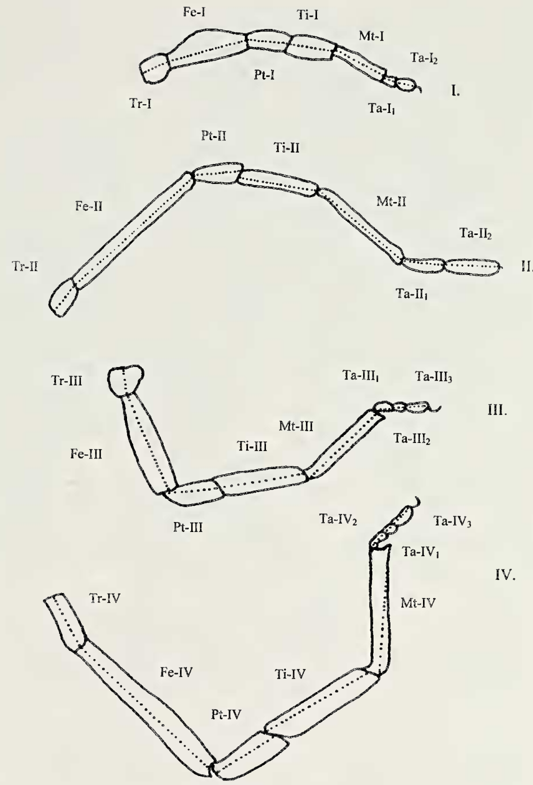

Figure 1.—Standardized measurements (dotted lines) of the leg articles in *T. nepaeformis*. I–IV = legs, Tr = trochanter, Fe = femur, Pt = patella, Ti = tibia, Mt = metatarsus, Ta = tarsus.

departure from normality was excluded from further analyses.

The RA measure was provided using the formula FA4 for the measure of FA according to Palmer (1994): RA = var (R–L), where "var" is the variance, and "R" and "L" are the right and the left item, respectively (Palmer & Strobeck 1986). The differences between sexes, and between damaged and undamaged individuals were tested using One Way ANOVA, the *F*-test for testing differences between means, and Levene's test for homogeneity of variances.

The centroid within the prosoma, based on the equal radial distance of the tips of both the longest, the 2nd and the 4th legs, nearly coincides with that based on the equidistance of the distal parts of the coxae, and was called the leg centroid. It was used in testing frequencies of damaged articles for their stochasticity. The body centroid is not appropriate for this purpose because in this way, the

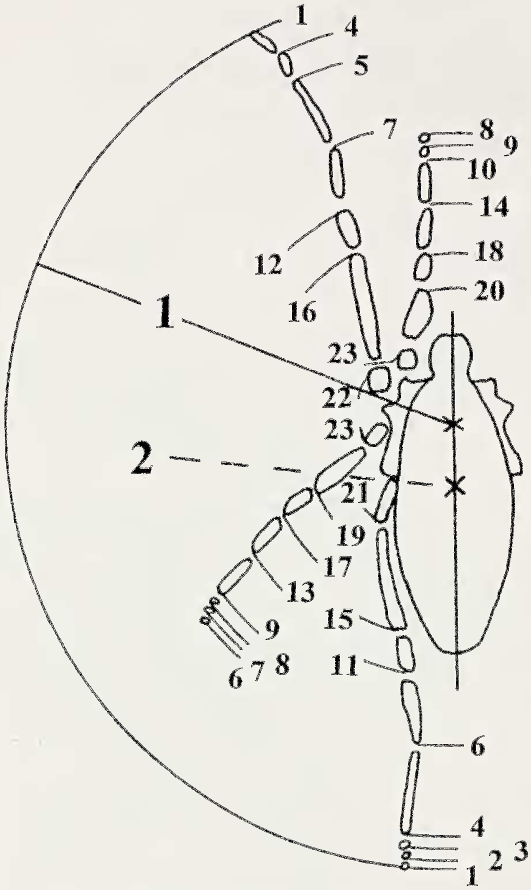

Figure 2.—The leg-centroid (1) and body-centroid (2) in *T. nepaeformis*. The range of danger risk, descending from 1 to 23, according to the leg-centroid.

first two leg pairs are a priori more exposed to physical dangers (Fig. 2). All leg articles (30 on each body side) were ranked into 23 classes of equally expected danger-risk, based on the radial distance of their distal parts from the leg centroid. For each leg, the correlation between the frequencies of injuries and the article lengths, and the expected risk and the realized frequencies of injuries was computed using the Pearson-product moment correlation. A chi square test was provided to analyze the differences between legs according to their injury frequencies. The computer software SPSS 11.0 (SPSS 2001) was used in all statistical procedures. The voucher specimens are deposited in the Slovene Museum of Natural History (Ljubljana).

RESULTS

In most populations, fewer than 5% of individuals were found injured. However, in three cases (Korte, Idrija, Tarcento) up to 20–30% of individuals had some injury. Fresh leg stumps were characterized by their ragged margins, and the healing ones by the brownish-black color of their injured tips. Article stumps reflecting old injuries, were of the usual color and with more or less regenerated, rounded tips. This way, in otherwise non-final articles (e.g., the 1st tarsus II, metatarsus and tibia), a smooth terminal chitin or a tip with a pseudonormal terminal-leg chaetotaxy, in some cases including an auxiliary claw, appeared. The final, damaged article was mostly shorter than the adequate opposite, undamaged one, but in a few cases elongation of the article was recorded. Regenerated damaged articles found in adults had most probably been severed in the juvenile and subadult stage. Some short articles, like the 1st, 3rd and 4th leg tarsi, were not injured.

Between–individual variation in nondirectional asymmetry of leg articles, except for trochanter II in females, was significantly larger than that of the measurement error (Table 1). On the other hand, the degree of asymmetry was larger than the degree of measurement error. We detected no evidence of DA; mean asymmetry in each trait was not significantly different from zero with an leptokurtic distribution, consistent with RA, but not with AS (Tables 2, 3).

The differences in R-L between sexes were not statistically significant in damaged specimens ($F_{1,94}$ = 0.01–3.79, P = 0.055–0.984); therefore the R-L data of both were pooled. The range of asymmetry in the lengths of the undamaged articles directly adjacent to the damaged ones was in 12 of 19 articles significantly larger in comparison to the undamaged specimens (Tables 2, 4, Fig. 3—case patella II), while tibia III shows a platykurtic distribution ($g_2 = -5.7$) (Table 3).

There was no significant correlation between the frequencies of injuries and the relative article lengths (r = 0.176, P = 0.352). As expected, the frequencies of injuries increased with increasing distance from the leg centroid (r = 0.970–0.995, $P < 0.001$). The frequencies of damage differed significantly between legs (chi square; $P < 0.001$), and de-

Table 1.—Mixed-model ANOVA of 14 leg characters (frequencies ≥ 3) of damaged legs in 67 randomly chosen individuals of *T. nepaeformis* chosen to analyze the measurement error.

Leg article	Male	Female
	F, P	*F, P*
Femur I	$F_{8,18}$ = 2.1, P = 0.045	$F_{10,22}$ = 50.25, P <0.0001
Patella I	$F_{6,14}$ = 21.47, P <0.0001	$F_{9,20}$ = 13.9, P <0.0001
Tibia I	$F_{5,12}$ = 35.72, P <0.0001	$F_{2,20}$ = 52.08, P <0.0001
Trochanter II	$F_{13,29}$ = 32.69, P <0.0001	$F_{6,14}$ = 1.33, P = 0.618
Femur II	$F_{14,28}$ = 5633, P <0.0001	$F_{6,14}$ = 227.1, P <0.0001
Patella II	$F_{9,21}$ = 41.12, P <0.0001	$F_{2,5}$ = 165.59, P <0.0001
Tibia II	$F_{8,19}$ = 55.38, P <0.0001	$F_{4,10}$ = 236.5, P <0.0001
Trochanter III	$F_{6,14}$ = 11.78, P = 0.0002	$F_{3,8}$ = 19.93, P = 0.0009
Femur III	$F_{5,12}$ = 36.77, P <0.0001	$F_{2,6}$ = 442.4, P <0.0001
Patella III	$F_{5,12}$ = 101.8, P <0.0001	$F_{2,6}$ = 34.0, P = 0.0001
Tibia III	$F_{5,12}$ = 6.19, P = 0.0092	No matches
Femur IV	$F_{3,9}$ = 39.63, P <0.0001	$F_{3,8}$ = 134.3, P <0.0001
Patella IV	$F_{3,9}$ = 126.78, P <0.0001	$F_{3,8}$ = 419.0, P <0.0001
Tibia IV	$F_{3,9}$ = 1295, P <0.0001	$F_{3,8}$ = 227.2, P <0.0001

creased from the 2nd, 1st, to the 3rd and the 4th legs (Tables 5, 6).

In the localities investigated for small mammals, hedgehogs were absent, and shrews were found to predate troguli: in 204 shrews, five opilionid and more than 14 other arthropod species were found. In two *Sorex araneus*, the remains of *T. nepaeformis* were recognized. No other predator of troguli was recorded, although moles and other occasional predators are believed to prey upon them, too.

DISCUSSION

While frequencies of less than 5% for leg damage in *T. nepaeformis* can have various causes, e.g., trampling, mechanical injury caused by falling stones etc., the larger percentage of injured individuals in other popu-

Table 2.—Kolmogorov-Smirnov's test (K-S) of distribution for normality and *t*-test for mean testing in *T. nepaeformis*. Levene's test of homogeneity of variances (One Way ANOVA: *F, P*) in undamaged and damaged specimens. (* P < 0.05; n.s. = no significant differences; / = no matches).

Leg article	K-S	*t*	*F*	*P*
Femur I	0.16 n.s.	−1.82 n.s.	0.60	0.439
Patella I	0.4 n.s.	−1.14 n.s.	42.54	<0.001
Tibia I	0.17 n.s.	0.20 n.s.	10.49	0.002
Metatarsus I	0.37*	−1.88 n.s.	14.50	<0.001
Trochanter II	0.24 n.s.	−0.13 n.s.	72.60	<0.001
Femur II	0.25 n.s.	0.34 n.s.	4.47	0.037
Patella II	0.23*	−0.91 n.s.	16.09	<0.001
Tibia II	0.32*	−1.15 n.s.	37.07	<0.001
Metatarsus II	0.17 n.s.	1.23 n.s.	30.80	<0.001
Trochanter III	0.27 n.s.	−1.10 n.s.	0.66	0.419
Patella III	0.19 n.s.	−0.71 n.s.	0.06	0.807
Tibia III	0.28 n.s.	−2.05 n.s.	19.85	<0.001
Metatarsus III	0.45*	−1.21 n.s.	35.46	<0.001
Tarsus III_1	0.38 n.s.	/	0.59	0.444
Tarsus III_2	0.25 n.s.	/	1.01	0.316
Femur IV	0.21 n.s.	−1.35 n.s.	0.18	0.674
Patella IV	0.21 n.s.	0.01 n.s.	39.08	<0.001
Tibia IV	0.27 n.s.	−0.01 n.s.	2.32	0.131
Metatarsus IV	0.23 n.s.	1.80 n.s.	59.12	<0.001

Table 3.—Statistical characteristics of leg articles length asymmetry in undamaged (n = 96) and damaged (n = 169) *T. nepaeformis*.

	Undamaged legs					Damaged legs					
Leg article	Mean	Variance	SE	Skewness	Kurtosis	n	Mean	Variance	SE	Skewness	Kurtosis
Trochanter I	0.008	0.002	0.005	0.225	−0.088	0					
Femur I	−0.027	0.006	0.008	−0.910	2.915	8	−0.055	0.007	0.030	−0.497	−1.199
Patella I	0.020	0.008	0.009	0.450	0.373	4	−0.212	0.139	0.187	−1.923	3.762
Tibia I	−0.005	0.005	0.007	−0.268	1.710	13	0.008	0.024	0.043	0.915	2.435
Metatarsus I	0.027	0.011	0.011	−0.315	0.552	13	−0.140	0.073	0.075	−2.544	6.698
Tarsus I1	0.002	0.001	0.003	−0.346	−0.204	1	−0.010				
Tarsus I2	0.008	0.001	0.004	−0.966	3.435	0					
Trochanter II	−0.003	0.004	0.006	0.106	0.237	10	0.167	0.141	0.119	1.391	1.248
Femur II	−0.035	0.005	0.007	0.131	−0.271	7	−0.003	0.017	0.050	−1.323	1.754
Patella II	0.014	0.014	0.012	0.049	0.779	26	−0.087	0.101	0.062	−1.228	3.550
Tibia II	0.005	0.005	0.007	0.207	0.578	15	−0.116	0.496	0.182	−1.336	3.504
Metatarsus II	0.057	0.015	0.013	0.612	1.030	17	0.060	0.181	0.103	−0.539	1.827
Tarsus II1	0.006	0.001	0.004	0.467	0.838	0					
Tarsus II2	0.012	0.004	0.006	1.496	4.152	0					
Trochanter III	−0.005	0.002	0.005	0.384	0.238	4	−0.045	0.007	0.041	−0.365	1.574
Femur III	−0.030	0.007	0.008	0.494	1.954	2	−0.065	0.014	0.085		
Patella III	0.023	0.012	0.011	0.104	0.376	6	−0.029	0.010	0.042	0.313	−0.571
Tibia III	0.009	0.018	0.014	−1.458	6.710	4	−0.375	0.133	0.183	0.002	−5.742
Metatarsus III	0.020	0.007	0.008	0.073	−0.444	7	−0.186	0.166	0.154	−2.609	6.852
Tarsus III1	0.003	0.001	0.003	0.276	−0.130	3	0.003	0.001	0.013	1.732	
Tarsus III2	0.004	0.001	0.003	−0.594	0.518	3	−0.017	0.000	0.009	0.935	
Tarsus III3	0.006	0.001	0.004	−0.333	0.971	0					
Trochanter IV	−0.014	0.004	0.007	0.095	0.419	2	0.074	0.017	0.091		
Femur IV	−0.017	0.009	0.010	0.198	1.286	4	−0.078	0.013	0.058	−0.803	0.659
Patella IV	0.052	0.018	0.014	−0.199	0.582	6	0.002	0.348	0.241	−1.250	1.818
Tibia IV	0.021	0.011	0.011	−0.366	1.712	6	−0.001	0.034	0.076	−1.699	3.286
Metatarsus IV	0.033	0.013	0.012	0.008	2.962	5	0.505	0.393	0.280	1.472	2.045
Tarsus IV1	0.009	0.001	0.004	−0.167	0.409	2	−0.005	0.001	0.025		
Tarsus IV2	0.010	0.001	0.002	−0.248	−0.403	1	−0.020				
Tarsus IV3	0.009	0.001	0.003	0.318	0.471	0					

lations might be the consequence of higher predation pressure. Short articles, like trochanter and most tarsal articles, were inappropriate in the analysis because of their low frequencies of injury, and higher level of measurement error, e.g., in a female trochanter II. The significantly larger RA in the damaged specimens, is assumed to be the direct consequence of the regenerative processes in the severed articles. Such damage has been recorded also in other *Trogulus* species.

Table 4.—Summary presentation of RA in legs of 169 damaged specimens of *T. nepaeformis* (+ = statistically significant differences; − = no significant differences; / = not taken into account). For abbreviations of leg articles, see Fig. 1.

Leg	Tr	Fe	Pt	Ti	Mt	Ta_1	Ta_2	Ta_3
I	/	−	+	+	+	−	/	
II	+	+	+	+	+	/	/	
III	−	/	−	+	+	−	−	/
IV	/	−	+	−	+	/	/	/

Table 5.—Frequencies of damaged legs in 169 *T. nepaeformis*.

	Males		Females		All	
Leg	n	n%	n	n%	n	n%
I	13	18.3%	26	26.5%	39	23.1%
II	33	46.5%	42	42.9%	75	44.4%
III	12	16.9%	17	17.3%	29	17.2%
IV	13	18.3%	13	13.3%	26	15.3%
Sum	71	100.0%	98	100.0%	169	100.0%

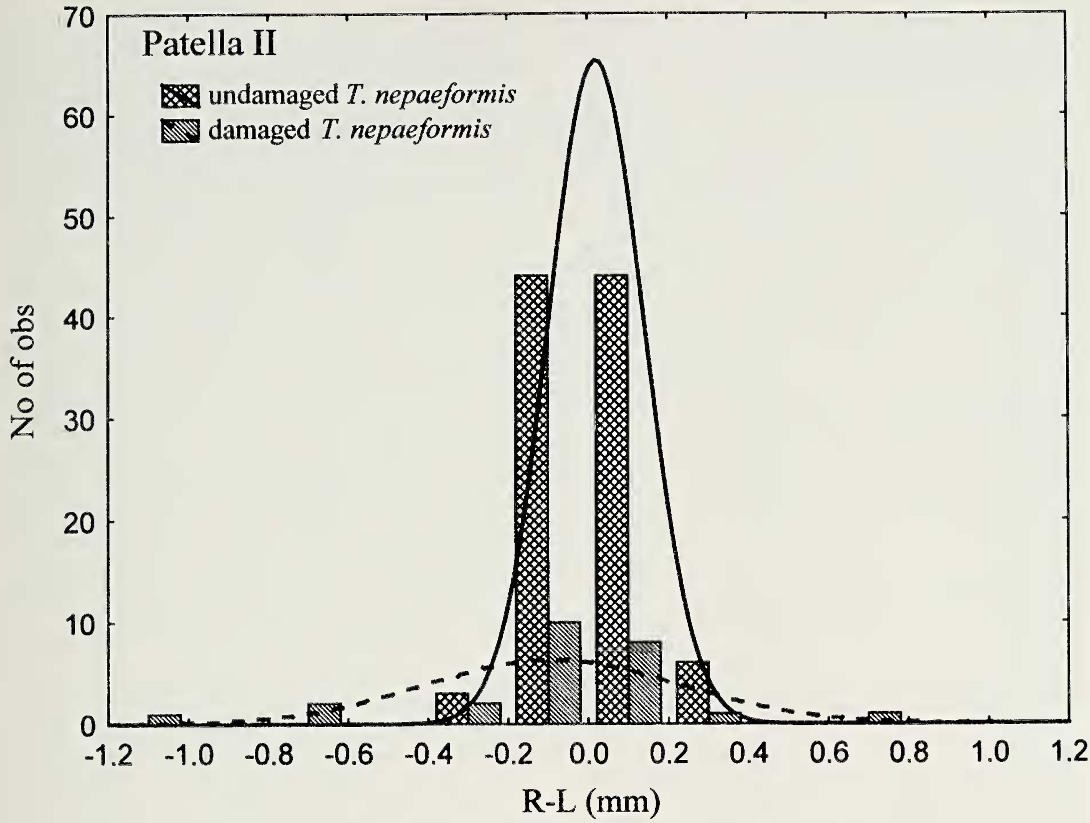

Figure 3.—Frequency distribution of R-L in patella II in damaged and undamaged *T. nepaeformis*.

In a few cases, elongation of the secondary end-article was recorded, resulting presumably either from fusion from the previous undamaged article with the rest of the damaged terminal one or by an anomalous repair. Ontogenetic abnormalities have rarely been reported in harvestmen, in Europe, e.g., by Hadži (1928) and Mitov (1995b). It seems likely that in *T. nepaeformis*, damage to the legs can induce anomalous growth in the stumps, especially during molting, a fact that could have been overlooked in other harvestmen.

The trochanter and the tarsal articles, except for tarsus II, are not appropriate for studying RA/FA in troguli because of their shortness and the consequent low frequencies of damage. There is no unequivocal explanation for the departure of tibia III in favor of AS, but this could be the consequence of the low frequency of occurrences of injury. As in *T. nepaeformis*, the injuries evoke measurement changes in the damaged, as well as in the previously undamaged articles.

The decreasing frequency of damage from the 2nd, 1st to the hind legs indicates that such injuries probably appear during the forward motion of troguli. It is assumed that most damage appears when troguli meet shrews within their common habitat while both are active. On such occasions, troguli normally simulate death and do not flee, thus minimizing total injury but receiving most injuries from the frontal side.

Probably the smooth, terminal chitin of the stump tips represents the first stage of regeneration, while the pseudonormal terminal-leg chaetotaxy and an auxiliary claw appear later. To confirm these interpretations, the regenerative process itself deserves to be studied in detail. This, and the role of harvestmen within the shrew diet will be analyzed elsewhere.

The influence of FA on mate choice has been found in a number of taxa (Uetz & Smith 1999). In night-active, ground inhabiting *T. nepaeformis* with small eyes, as well as in other edaphic harvestmen, vision has no important role. In *Trogulus* species, tactile and chemical senses promote the communication

Table 6.—Number of injured articles, cumulative number of injuries per leg, relative article lengths and range of danger risk per leg (descending from 1 to 23, according to the leg centroid) used in testing the stochasticity of injuries in *T. nepaeformis*.

Leg article	*n* of injured articles	Cumulative *N* of injuries/leg	Relative article length	Range of danger risk/leg centroid
Trochanter I	0	0	2	23
Femur I	8	8	5	20
Patella I	4	12	3	18
Tibia I	13	25	5	14
Metatarsus I	13	38	5	10
Tarsus I_1	1	39	1	9
Tarsus I_2	0	39	1	8
Trochanter II	10	10	3	22
Femur II	7	17	14	16
Patella II	26	43	5	12
Tibia II	15	58	6	7
Metatarsus II	17	75	9	5
Tarsus II_1	0	75	3	4
Tarsus II_2	0	75	3	1
Trochanter III	4	4	3	23
Femur III	3	6	8	19
Patella III	6	12	4	17
Tibia III	4	16	5	13
Metatarsus III	7	23	5	9
Tarsus III_1	3	26	1	8
Tarsus III_2	3	29	1	7
Tarsus III_3	0	29	1	6
Trochanter IV	2	2	5	21
Femur IV	4	6	13	15
Patella IV	6	12	4	11
Tibia IV	6	18	8	6
Metatarsus IV	5	23	11	4
Tarsus IV_1	2	25	1	3
Tarsus IV_2	1	26	1	2
Tarsus IV_3	0	26	1	1

between sexes Pabst (1953). Troguli pose the opportunity to study the influence of RA on tactile and chemical cues interacting between sexes.

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